

PHOTOSYNTHETIC RESPONSE OF CHRYSANTHEMUM UNDER DIFFERENT WATER REGIMES

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Potted chrysanthemums were subjected to drought and water stress treatments. The experiment included four treatments with different level of the substrate saturation. The net photosynthesis rate, stomatal conductance, transpiration rate and intracellular CO₂ were measured by the infrared gas analysis method. The study confirmed the trend of decreasing physiological parameters (P_n , g_s , E, Ci) with reduced water availability in the substrate. The reduced water availability significantly reduced stomatal conductance, transpiration, intracellular CO₂ concentration and, subsequently, photosynthesis. Continuous flooding significantly reduced photosynthesis and non-significantly increased transpiration and intracellular CO₂ concentration. The possible acclimatization of the plants to subsequent water deficit conditions was studied, too. Following the drying cycle, efficient and fast recovery of chrysanthemum plants was observed.

Keywords: ornamental plants, photosynthesis, P_n, transpiration, water stress

1 Introduction

In commercial nursery production systems, frequent and severe drought stress of container-grown plants can reduce crop quality, delay marketing, and, consequently, profitability. *Chrysanthemum* is one of the leading ornamental flowers worldwide, and its production faces a variety of challenges under environmental stress conditions (Chen et al., 2012). Drought stress is one of the most harmful types of stress, because it retards chrysanthemum growth. Hence, it is essential to improve the tolerance of chrysanthemum to this type of stress in order to achieve sustainable production (Satapathy et al., 2014).

Many papers are focused on the response of the plant to a single period of drought stress. These treatments are aimed either at dwarfing plants (Roeber et al., 1995), or describe a specific response of the leaf tissue to a period of wilting (Wang and Clarke, 1993). Water deficits occur when transpiration exceeds water uptake. Plants conserve water by reducing their transpiration rates by such mechanisms as modifying stomatal behaviour or in the long-term by reducing leaf area (Blum, 1996). The plants tolerant to drought stress show different adaptation mechanisms to overcome drought stress, including morphological, physiological, and biochemical modifications. These responses include increasing root to shoot ratio, growth reduction, changes of the leaf anatomy, reduction of leaf size and the total leaf area to limit water loss and guarantee photosynthesis (Toscano et al., 2019).

Techniques for measuring plant water status and inducing water stress in plants are well established. However, due to the dynamic nature of water deficits remains extremely difficult. These difficulties are enhanced when a water deficit occurs rapidly, for example when there is a limited supply of water in small pots combined with high evaporation by a flowering plant. Under such conditions, stomata may close due to low water availability in the soil - and yet leaf water potential (Ψ_i) may remain high (Davies and Zhang, 1991). According to Long and Bernacchi (2003) the infrared gas analysis (IRGA) is the only current method of widespread importance for measuring photosynthesis. These portable systems provide real-time measurement of CO₂ uptake, transpiration, stomatal conductance and map intercellular CO₂ mole fraction. The aim of the study was to determine the influence of different water irrigations to physiological parameters of chrysanthemum plants by the infrared gas analysis method. The supposed contribution was

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to optimize production conditions related to irrigation of chrysanthemum plants.

2 Material and methods

Potted chrysanthemum plants Dendranthema indicum (L.) Desmoulins 'Surf' were grown in peat: perlite (Pindstrup substrate number 2, Mosebrug A/S) with one cutting per 10.5 cm pot in a growth chamber with constant conditions (temperature 20 °C, 60% relative humidity, 14 h light/10 h dark photoperiod, PPFD 500 μ mol/m²/s). The experiment started 25 days after the collection of cuttings from mother plants and lasted for a month. The experiment included four treatments with different availability of water. Water loss (evapotranspiration) was recorded on a daily basis with an electronic scale, for each pot individually. The control plants were irrigated individually everyday in the morning according to the weight loss since last irrigation, in order to obtain pot water holding capacity. Based on daily water consumption, control plants (variant K) were top-watered daily with amount of water (nutrient solution containing N at 286, P at 30, K at 359, Ca at 139, Mg at 21 and SO₄ at 42 ppm, EC 2.46, pH 5.8) equal to 100% of evapotranspiration. Other treatments included three different levels of water availability: continuous water deficit (variant A), cyclic water deficit (variant B) and continuous flooding (variant C). Continuous water deficit plants were given an amount of nutrient solution equal to 40% of the mean daily water consumption of control plants. The cyclic water deficit treatment was a repeating nonlethal cyclic water deficit treatment, where watering was withheld for 1 day - 24 h (variant B2) and recovery phases where the plants received the same amount of water and nutrient solution as control plants (variant B1). The experiment included 15 cycles of water deficit treatments in total. Continuous flooding (variant C) simulated overwatering plants. The pot trays were kept with permanent irrigation up to 3 cm of height minimally. Every day the trays were cleaned and irrigated with new nutrient solution to protect plants against fungal pathogens. There were 8 plants in each treatment.

The net photosynthesis rate (P_n) , stomatal conductance (g_s) , transpiration rate (E) and intracellular CO_2 concentration (Ci) were measured every day on single leaves of each plant with a differential CO_2/H_20 infrared gas analyzer CIRAS-1 (PP-Systems, Hitchin, UK). Gas exchange measurements of leaves were made on the most recently fully expanded leaf at photosynthetic photon flux density 500 µmol/ m²/s, leaf temperature

at 25 °C, vapour pressure deficit (VPD) at 15mbar and ambient CO₂ concentration of 400 ppm. Once the leaf was placed in the cuvette, the plant was left a further 20 min to stabilize before any measurements were recorded and each data points represented the mean of 3–5 min at steady-state. The statistical analyses were done using the SigmaStat software. ANOVA (Kruskal-Wallis one way analysis of variance on ranks) and pairwise multiple comparison procedures (Tukey test) were tested for significance at p < 0.05.

3 Results and discussion

ANOVA analyses confirmed significant differences between P_n of control plants compared to the plants grown with 40% water availability. Reduced irrigation induced 59.35% lower net photosynthesis rate compared to the control irrigation. A significant difference was also confirmed between P_n of control plants compared to the plants with cyclical watering. The photosynthesis of plants with cyclical watering in days without watering decreased – by 49.85% and on days after re-watering P_n decreased – by 19% compared to the control plants. There were confirmed significant differences of P_n for plants within cyclical watering treatment. Plants after re-watering reached by 37.9% higher P_n compared to the days without watering.

Non-significant differences were observed between P_n of cyclically watered plants during the days without watering and plants with 40% reduced water availability. Cyclically watered plants during days without watering reached about 18.5% higher values of P_n compared to the plants with 40% reduced water availability. There were found significant differences in P_n of the control plants and plants with continuous supply of water. Flooding irrigation caused 10.5% decrease of P_n compared to the controls. Non-significant differences were determined between P_n of plants with continuous supply of water and cyclically watered plants in days after re-watering. P_n of plants with continuous supply of water was 10.4% higher compared to the plants with cyclical watering. However, highly significant differences were confirmed between P_n of plants with continuous supply of water and plants with 40% water availability and also between P_n of plants with continuous supply and cyclically watered plants after non-watering. Dehydrated plants with 40% water availability showed 54.6% decrease of P_n compared to the plants with continuous supply of water and cyclically watered plants after non-watering showed 44.2% decrease of P_n compared to the plants with continuous supply of water. Table 1 shows the changes

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of P_n in the course of drought, cyclical watering and flooding during the experiment.

Effects of water stress on photosynthetic decrease of ornamental plants have been well-documented in many reports: Gazania rigens (Gao et al. (2016), garden roses (Niu and Rodriguez, 2009), ornamental shrubs Photinia × fraseri and Eugenia uniflora (Toscano et al., 2016), Callistemon laevis (Álvarez et al., 2011). The debate as to whether drought mainly limits photosynthesis through stomatal closure or through metabolic impairment has been running since the earliest reports on the effects of drought on photosynthesis (Flexas and Medrano, 2002). During the last decade, stomatal closure was generally accepted to be the main determinant for decreased photosynthesis under mild to moderate drought (Ort et al., 1994). Comparing results from different authors is complex due to interspecific differences in the response of stomatal conductance and photosynthesis to leaf water potential and/or relative water content, the parameters most often used to assess the degree of drought (Medrano et al., 2002). It is clear that stomata close progressively as drought progresses, followed by parallel decreases of net photosynthesis.

Plants would be more vulnerable to water stress after rewatering or a cycled water environmental change, which occur more frequently under climatic change conditions in terms of the prediction scenarios. Plant growth, photosynthesis and stomatal aperture may be limited under water deficit, which would be regulated by physical and chemical signals. Under rewatering, the recovery of plant growth and photosynthesis would appear immediately through growing new plant parts, re-opening stomata, and decreasing peroxidation; the recovery extents (reversely: pre-drought limitation) due to rewatering strongly depend on pre-drought intensity, duration and species. Understanding how plants respond to episodic drought and watering pulse and the underlying mechanism, it is remarkably helpful to implement vegetation management practices under the conditions of climate change (Xu et al., 2010).

The results of ANOVA confirmed high significant difference in stomatal conductance between control and stressed plants with 40% water availability and also between control and both variants of cyclically stressed plants. Stomatal conductance of stressed plants with different watering regimes decreased from 75.6% to 28% (Table 1). Non-significant difference was observed between g_s of overwatered plants compared to the controls and also between g_s of cyclically watered plants after non-watering compared to the plants with 40% water availability.

As reported in several studies, water stress decrease of stomatal conductance was observed in Olea europaea (Chartzoulakis et al., 1999), Morus alba (Ramanjulu et al., 1998), and pot roses (Riseman et al., 2001). In many species, reduction in stomatal conductance with increased water stress may limit diffusion of CO₂ to chloroplasts and, consequently, net photosynthetic rate (Lawlor, 2002). Stomatal regulation plays a key role in gas exchange between vegetation and atmosphere interface. Ninety percent loss of plants is from transpiration thought stomatal opening (Wang et al., 2009). On the other hand, stomatal limitation would be recognized as a major factor for photosynthetic reduction when available water become scant, while non-stomatal limitation such as decreases in Rubisco activity, CO₂ availability in the chloroplast and PSII photochemistry efficiency is progressive gradual with water stress intensity and persistence duration (Xu et al., 2009).

Williams et al. (2000) studied the effect of reducing production water availability during cultivation on the post-production quality of potted miniature roses (*Rosa* \times *hybrida*). Plants grown with cyclical water availability tolerated subsequent water stress better than plants produced with a constant supply of water, irrespective of whether the constant supply of water was adequate or not. Another study with

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Treatment	<i>P_n</i> (μmol/m²/s)	<i>E</i> (μmol/m²/s)	<i>g</i> ₅ (μmol/m²/s)	<i>Ci</i> (ppm)		
Variant K	14.06 ±0.25a	3.058 ±0.118a	288.4 ±10.4a	266.1 ±3.86a		
Variant A	5.72 ±0.41b	0.967 ±0.101b	70.3 ±9.7b	203.3 ±7.69b		
Variant B1	11.28 ±0.53c	2.641 ±0.141a	207.6 ±12.8c	252.1 ±8.22a		
Variant B2	7.01 ±0.64b	1.155 ±0.257b	86.3 ±21.5b	200.2 ±13.04b		
Variant C	12.59 ±0.32ac	3.095 ±0.089a	277.9 ±7.1a	267.8 ±4.54a		

Table 1	Physiological	characteristics	of chr	ysanthemum	with	different	water	treatment
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 P_n – photosynthesis, E – transpiration, g_s – stomatal conductance, Ci – intracellular CO₂ concentration, K – control, A – plants with 40% water availability of control, B – cyclic water deficit (B1 – days after re-watering, B2 – days without watering), C – continuous flooding. The same letter within each column indicates no significant difference among treatments ($P \le 0.05$) according to the Tukey's test



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roses (Riseman et al., 2001) also confirmed that reduced water availability during the production of potted miniature roses improves water use efficiency, tolerance to subsequent drought stress and improves post-production performance. The two rose cultivars used different mechanisms to respond to drought. Apollo utilized osmotic adjustment while Charming modified stomatal closure.

In our study, reduced water availability also significantly influenced transpiration rate. Control plants transpired at a higher rate (+64.8%) compared to the plants with 40% water availability and at a higher rate (+62.2%) compared to the cyclically watered plants during the days without watering (Table 1). It has been reported in pot roses (Williams et al., 2000) that the cyclically-grown plants were able to restore transpiration and net photosynthesis during times of recovery similar to, but not equal to the control plants. The difference in transpiration was not significant between control and cyclically watered plants after rewatering; control plants reached higher transpiration rate (+13.6%) compared to the cyclically watered plants after rewatering. Flooding had no significant influence on E as well; overwatered plants reached by 1.2% higher transpiration rate than the controls (Table 1).

In order to estimate the tolerance to drought stress in plants, the transpiration ratio is essential. In fact, it has been observed that species that can retain a greater quantity of water and therefore lose less water through the stomata are more tolerant to drought (Riaz et al., 2013). As reported by Galmés et al. (2007), shrubs have a better ability to regulate transpiration compared to herbaceous plants. Soil drought stress decreases the leaf water potential, which reduces the swelling pressure and subsequently, stomatal closure. Plants experience water stress when the rate of transpiration becomes very high or when the water supply to roots become difficult (Reddy et al., 2004). Wang et al. (2006) observed a strong correlation of stomatal conductance with transpiration compared to net photosynthesis. This could be due to the soil moisture stress-induced abscisic acid (ABA) which is stimulated by soil drying through the transpiration stream resulting in stomatal closure.

Wang et al. (2006) detected that when soil water content dropped below 47% of field water capacity, the leaf water potential decreased rapidly, indicating a significant threshold reaction of soybean leaves about -1.02 MPa. Below this, the leaf water potential and net photosynthesis ratio dropped rapidly. When the soil water content was 47%, the leaf water potential and net photosynthesis ratio were nearly as high as those in CK, but the transpiration ratio was by 67% lower, indicating that transpiration was more sensitive to drought than photosynthesis. After rewatering, the water status of soybean leaves improved, the net photosynthesis ratio and transpiration ratio increased linearly, and leaf stomatal conductance also recovered quickly.

Reduced water availability induced significant decrease in intracellular CO_2 concentration (*Ci*) of plants with 40% water availability (-23.6%) compared to the control and cyclically watered plants during the days without irrigation (-24.8%) compared to the control. Within cyclical treatment, after periodic alternation of water deficit and re-watering *Ci* decreased and increased repeatedly. Re-watering of plants significantly increased *Ci* (+20.6%) compared to the non-watering. Both treatments, re-watering of cyclically watered plant and flooding, non-significantly influenced *Ci* compared to the control. Re-watering decreased *Ci* (-5.3%) and overwatering increased *Ci* (+0.6%) compared to the control (Table 1).

The influence of *Ci* on stomatal conductance was already reported (Cornic, 2000). In a study conducted by Toscano et al. (2018) on shrubs *Lantana* and *Ligustrum*, the analysis of leaf anatomical traits allowed the identification of the different strategies used during water stress conditions. During severe deficit of irrigation, *Lantana* plants increased spongy tissue rather than the palisade tissue; this anatomical modification facilitated the diffusion of CO_2 towards the fixation sites in order to increase the concentration gradient between internal air space and the atmosphere, thus enhancing the competition among cells for CO_2 and light (Fraser et al., 2009).

Chen et al. (2018) investigated that net photosynthetic rate, stomatal conductance, water use efficiency and transpiration rate in the non-grafted chrysanthemums were significantly decreased. Moreover, the intercellular CO₂ concentrations were significantly increased compared to the grafted plants at 5 and 6 d following drought stress. Non-grafted chrysanthemums were less able to resist dehydration, and repressed the genes encoding the expression of photosynthetic components. Using *Artemisia annua* grafts could alleviate drought stress in chrysanthemums by improving gas exchange capacity and maintaining *CmrbcL, CmrbcS, Cmcab* and *CmpsaB* gene expression, thereby increasing Rubisco activity and improving photosynthetic performance.

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4 Conclusion

The study described sensitivity of physiological parameters to different water availability treatments. Reduced water availability significantly reduced stomatal conductance, transpiration, intracellular CO₂ concentration and, subsequently, photosynthesis. Continuous flooding significantly reduced photosynthesis and non-significantly increased transpiration and intracellular CO₂ concentration. The study confirmed resistance of chrysanthemum plants to cyclical water deficit. Following the drying cycle, efficient and fast recovery of the plants was observed. Monitored reduced water availability during the production of potted chrysanthemum plants can improve tolerance to subsequent drought stress and post-production performance. This result can be practically applied for indoor plant maintenance. Chrysanthemum plants can be better adapted to the water stress, when they are not irrigated regularly with less amount of water. The modulating irrigation with absence of watering for short periods can enhance their adaptability to drought.

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